

THE ERGONOMICS OF CASTE IN THE SOCIAL INSECTS

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Past studies of caste systems in the social insects have focused on the obvious genetic and physiological problems of the mechanisms that control caste determination in the individual insect. Several independent experimental investigations have now provided a body of definitive information on the subject. In the great majority of bees, and in most—and perhaps all—ants, wasps, and termites, caste is apparently environmentally determined. The environmental controls are diverse in nature and differ from group to group. They include the biasing influences of yolk nutrients, of various quantitative and qualitative factors in larval feeding, of temperature changes, and of the caste-specific pheromones (see reviews by Brian, 1965; Lüscher, 1961; Weaver, 1966).

There is a second major problem connected with caste which is evolutionary in nature and can be phrased as follows: Why do the *ratios* of the castes (in a whole colony population) vary among species of social insects? This question is much less obvious than the physiological one and can be considered only in the context of the ecology of the individual species. A large amount of empirical information on ratios exists but only a small amount of theory. Only recently have students of social insects begun to handle the subject in a systematic fashion, as, for example, in the work of Richards and Richards (1951), Lindauer (1961), Hamilton (1964), Brian (1966), and Wilson (1966). Still, very little theory on the subject has been formulated.

This matter of the presence or absence of a given caste, together with its relative abundance, when present, should be susceptible to some form of optimization theory, provided we are able to assume selection at the colony level. In fact, colony selection in the advanced social insects does appear to be the one example of group selection that can be accepted unequivocally. It therefore seems a sound procedure to accept colony selection as a mechanism and to press on in search of an optimization theory based on the axiom that the mechanism operates generally. For if selection is mostly at the colony level, workers can be altruistic with respect to the remainder of the colony; and their numbers and behavior can be regulated to achieve maximum colony fitness. What has been lacking so far is an entree to the theory of group behavior, a way of abstracting our empirical knowledge of caste and colony ergonomics¹ into a form that can be used to analyze optimiza-

¹In an earlier article (Wilson, 1963) I suggested the term "ergonomics," borrowed from human sociology, to identify the quantitative study of the distribution of work, performance, and efficiency in insect societies.

tion. The purpose of this article is to show the feasibility of a first formulation by means of the techniques of linear programming and to report on some interesting but still imperfect and mostly theoretical results that have been obtained.

A LINEAR PROGRAMMING MODEL

The Concept of Cost

As colonies grow, their caste ratios change. Very young colonies founded by single queens typically consist solely of the queens and minor workers. As they approach maturity, these same colonies may add medias and major workers (also known as soldiers). Finally, they produce males and new, virgin queens. Here we will consider the ergonomics of the mature colony alone. A mature colony is defined as a colony large enough to produce new, virgin queens. Also, for convenience, we will include under the term "caste" both *physical castes*, such as minor workers and soldiers, and *temporal "castes."* The latter are classes of individuals in those periods of labor specialization which most individual social insects pass through in the course of their lives. What determines the efficiency of the mature colony is the number of workers in each temporal caste at any given moment. This conception is spelled out in the examples given in Figure 1.

Consider the mature colony. Depending on the species, the adult force may contain anywhere from a few tens of workers to several millions. The number is a species characteristic. It has been evolved as an adaptation to ultimate limiting factors in the environment. An ultimate limit may be imposed by a peculiar nest site to which the species is adapted, or a restricted productivity of some prey species on which the species specializes, or conversely, a prey species or competitor so physically formidable as to require a large worker force as a minimum for survival. These and other ultimate, limiting factors have already been documented and discussed in the literature (Brian, 1966). The mature colony, on reaching its predetermined size, can be expected to contain caste ratios which approximate the *optimal mix*. This is simply the ratio of castes which can produce the maximum rate of production of virgin queens and males while the colony is at or near its maximum size.

It is helpful to think of a colony of social insects as operating somewhat like a factory inside a fortress. Entrenched in the nest site, harrassed by enemies and uncertain changes in the physical environment, the colony must send foragers out to gather food while converting the secured food inside the nest into virgin queens and males as rapidly and as efficiently as possible. The rate of production of the sexual forms is an important component of colony fitness. Suppose we are comparing two genotypes belonging to the same species. If we could but measure survival rates of queens and males belonging to the two genotypes from the moment they leave the nests on

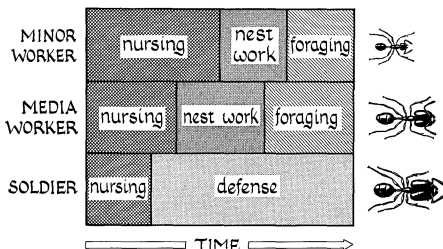


FIG. 1.—This diagram visualizes the principal work periods traversed in the life spans of three worker subcastes of a generalized polymorphic ant species. The work periods are those periods in which the indicated task is the most frequent one performed; other tasks may be performed at lesser frequencies. The form of the castes and the sequences of work periods within each caste are based on real species, but the precise durations of the periods are imaginary. In this case each of the eight periods, the (arbitrary) total encountered in the three castes, is treated as a separate "caste." The optimal mix can be evolved both by varying the relative numbers in each subcaste and the relative time spent in each work period. (The ants represented in this and subsequent figures belong to the myrmicine genus *Pheidole* and are shown here as an intuitive aid for the reader not very familiar with social insects.)

their nuptial flights, then record their mating success and the survival rate of the fecundated queens thereafter, together with the growth rates of the colonies the survivors produce, then we could calculate the relative fitness of the two genotypes. However, in order to develop an ergonomic theory in a stepwise fashion, we need now to restrict our comparison to the mature colonies. In order to do this and retain precision, we would have to do the following: take the difference in survivorship between the two genotypes outside the period of colony maturity and reduce it to a single weighting factor. But we can sacrifice precision without losing the potential for general qualitative results by taking the difference as zero. Now we are concerned only with the mature colony, and the production of sexual forms is (keeping in mind the artificiality of our convention) the exact measure of colony fitness. If colonies belonging to one genotype contain on the average 1,000 sterile workers and produce 10 new, virgin queens in their mature life span, and colonies belonging to the second genotype contain on the average only 100 workers but produce 20 new, virgin queens in their mature life span, the second genotype has twice the fitness of the first, despite its smaller colony size. As a result, selection would eliminate larger colony size.

The lower fitness of the first could be due to lower survival rate of mature colonies, or to a smaller average production of sexual forms per surviving mature colony, or to both. The important point is that the rate of production of sexual forms is the measure of fitness, and evolution can be expected to shape mature colony size and organization to maximize this rate.

The production of sexual forms is determined by the number of mistakes made by the mature colony as a whole in the course of its fortress-and-factory operations. A mistake is made when some potentially harmful contingency is not met—a predator successfully invades the nest interior, a breach in the nest wall is tolerated long enough to desiccate a brood chamber, a hungry larva is left unattended, and so forth. The cost of the mistakes for a given category of contingencies is the product of the number of times a mistake was made times the reduction in queen production per mistake. The total cost of all mistakes in a given period of time is visualized as the principal component in the reduction of colony fitness. In symbols,

$$\Delta N_f = f(W - W_m) - \sum_i F_i, \text{ and}$$

$$F_i = k_i x_i, \text{ where}$$

ΔN_f is the number of queens produced in a unit of time, say in one full year;

W is the weight of workers present during the rearing of the brood;

W_m is the minimum weight of workers required to rear virgin queens;

F_i is the cost (in number of virgin queens not produced) due to all errors in the i th error category;

x_i is the cost (in number of virgin queens) per error in the i th error category;

k_i is the frequency of errors in the i th error category.

The Lowest Tolerable Cost as a Uniform Value

At this early point, an interesting deduction can already be made concerning the behavioral responses of colonies to contingencies and the cost level tolerated by the colony. In brief, it can be argued that there is some threshold cost F at or above which the species evolves a behavioral response to hold the average cost (per colony per unit time) to F . Also, in cases where behavioral responses have been evolved, the cost tolerated per error category by the colony is in each case the same, namely, F . In other words, $F = F_1 = F_2 = \dots$ *et seq.* for each error category to which a discrete behavioral response has been evolved. This convergence effect is inferred as follows. If $F_i > F_j$ for any two error categories i and j , the colony is more likely to increase fitness with the same amount of behavioral evolution by decreasing F_i than by decreasing F_j . As F_i is decreased, F_j will decrease more slowly; or, more likely, it will remain about the same or increase, providing the alteration of behavior to respond to contingency i adversely affected its ability to respond to j . As a result, F_i and F_j will tend to converge.

Not all contingencies will be frequent enough, or costly enough, to prompt the evolution of a specific behavioral response; in other words, their total cost will not exceed F . For example, it is natural to expect alarm communi-

ation and attack behavior specifically adapted to arthropodan intruders, but no particular behavioral adaptation to avoid having meteorites fall on the nest.

Suppose a new contingency a arose through a change in the environment, and $F_a > F$. The behavior of the colony would tend to evolve to bring F_a equal with the other F_i ($\approx F$). This is not to say that F is an absolute threshold. The adjustment to a or any increase in the cost of another category (F_i) due to a change in the environment would cause readjustment in F_i values generally and a new convergence to some value F . But the new F might be different from the old.

The Two-Contingency Case

The average output of queens is viewed as the difference between the ideal number made possible by the productivity of the foraging area of the colony and the number lost by failure to meet some of the contingencies. The evolutionary problem that we are postulating to have been faced by social insects can be solved as follows: the colony produces the mixture of castes which maximizes this output. In order to describe the solution by means of a simple linear programming model, it is necessary to restate the solution in terms of the dual of the first statement: the colony evolves the mixture of castes that allows it to produce a given number of queens with a minimum of workers. The objective, as I have formulated it here, is to minimize the energy cost.

The main purpose of the section to follow is to show that under a wide variety of conceivable conditions the proportions of castes can be related to minimum energy cost in a linear form.

Let us start with the case of two contingencies whose costs would exceed the threshold value if left unattended, together with two castes whose efficiencies at dealing with the two contingencies differ. The inferences to be made from this simplest situation can then be extended to any number of contingencies and castes.

The most important step is to relate the total weights, W_1 and W_2 , of two castes at a given instant to the frequency and importance of two contingencies and the relative efficiencies of the castes at performing the necessary tasks. By stating the problem as the minimization of energy cost, the relation can be given in linear form as follows:

$$W_1 = \text{const (1)} - \frac{\alpha_{12} \ln(1 - q_{12})}{\alpha_{11} \ln(1 - q_{11})} W_2, \quad q_{11} > 0; \quad (1a)$$

$$W_1 = \text{const (2)} - \frac{\alpha_{22} \ln(1 - q_{22})}{\alpha_{21} \ln(1 - q_{21})} W_2, \quad q_{21} > 0; \quad (1b)$$

where const (1), const (2), and the coefficients of W_2 are constants determined by the frequency of occurrence and the importance of the contingencies, and by the relative efficiencies of the castes at meeting the con-

tingencies. These two expressions give the relative numbers of caste 1 and caste 2 needed to hold costs (due to the two contingencies, respectively) to the tolerable level. It will now be shown how they are derived and why it is reasonable to employ linear relationships in the exploratory phase of ergonomic theory. The following conventions will be used:

- W_1 is the weight of all members in an average colony belonging to caste 1;
 W_2 is the weight of all members in an average colony belonging to caste 2;
 F_1 and F_2 are the highest tolerable costs due to contingencies 1 and 2 (and by an earlier argument, $F_1 \approx F_2$);
 α_{11} is a constant such that $\alpha_{11}W_1$ gives the average number of individual contacts with a contingency of type 1 by members of caste 1 during the existence of the contingency;
 α_{12} is a constant such that $\alpha_{12}W_2$ gives the average number of individual contacts with a contingency of type 1 by members of caste 2 during the existence of the contingency;
 α_{21} and α_{22} are constants similar to the above two but with reference to contingencies of type 2;
 q_{11} is the probability that, on encountering contingency 1, a worker of caste 1 responds successfully;
 q_{12} is the probability that, on encountering contingency 1, a worker of caste 2 responds successfully;
 q_{21} and q_{22} are the probabilities similar to the above two but with reference to contingency 2;
 x_1 and x_2 are the average costs (in nonproduction of virgin queens) per failure to meet contingencies 1 and 2, respectively;
 k_1 and k_2 are the frequencies of contingencies 1 and 2, respectively, for a given period of time.

When a worker of, say, caste 1 encounters a contingency of type 1, the probability that it will respond incorrectly is $1 - q_{11}$. This value can be put to use only if we know the number of encounters per caste. Now if we label as p_{10} the probability that no worker of caste 1 encounters a given contingency of type 1, p_{11} as the probability that exactly one worker encounters it, p_{12} as the probability that exactly two workers encounter it, and so forth, then the probability that no correct response will be made to a given contingency of type 1 is

$$p_{10}(1 - q_{11})^0 + p_{11}(1 - q_{11}) + p_{12}(1 - q_{11})^2 + \dots,$$

and the cost in a given interval of time is this sum, multiplied by the frequency the contingency occurs, multiplied in turn by the cost of each contingency that is not successfully met:

$$k_1 x_1 \sum_i p_{1i}(1 - q_{11})^i.$$

The distribution of p_{1i} should be obtainable by empirical measurements; and very likely it can then be approximated by some general form, such as the Poisson. For our purposes, we can approximate the expression

$$\sum_i p_{1i}(1 - q_{11})^i$$

by a single number, which in turn is a function of W_1 , the weight of caste 1

in the colony. In the simplest case, the single most appropriate number is the mean value of i , that is, the mean number of contacts per contingency, which value can be labeled \bar{i} . Keeping in mind that \bar{i} is only an approximation of

$$\sum_i p_{i1}(1 - q_{i1})^i,$$

we next recognize that it must be a function of the number of workers of caste 1 present, or, translated into terms of the present model, of the total weight (W_1) of workers of caste 1. If the nest volume were kept constant and W_1 increased, the number of contacts per contingency by members of caste 1 should increase linearly; in other words, \bar{i} should be approximated by $\alpha_{11}W_1$, where α_{11} is a constant. In this case, the probability that caste 1, in the absence of caste 2, would not solve the contingency is about $(1 - q_{11})^{\alpha_{11}W_1}$; and the probability that caste 2, in the absence of caste 1, would not solve the contingency is about $(1 - q_{12})^{\alpha_{11}W_1}$. Let us now assume that the castes operate independently of each other in meeting contingencies. That is, the presence of caste 2 does not enhance or diminish the capacity of a given worker belonging to caste 1 to deal with a single given contingency of type 1. This is probably not always the case, but on the basis of my own subjective impressions I believe it is close enough to the truth in most behavioral interactions to be accepted as an approximation. Where it applies, the cost due to contingency 1 in a given period of time is given as follows:

$$F_1 \doteq k_1 x_1 (1 - q_{11})^{\alpha_{11}W_1} (1 - q_{12})^{\alpha_{11}W_1} \quad \begin{matrix} q_{11} > 0, \\ q_{12} > 0. \end{matrix} \quad (2a)$$

And, symmetrically,

$$F_2 \doteq k_2 x_2 (1 - q_{21})^{\alpha_{11}W_1} (1 - q_{22})^{\alpha_{11}W_1} \quad \begin{matrix} q_{21} > 0, \\ q_{22} > 0. \end{matrix} \quad (2b)$$

By rearrangement of the two formulas, *contingency curves* are obtained:

Contingency Curve 1

$$W_1 \doteq \frac{\ln F_1 - \ln k_1 x_1}{\alpha_{11} \ln (1 - q_{11})} - \frac{\alpha_{12} \ln (1 - q_{12})}{\alpha_{11} \ln (1 - q_{11})} W_2. \quad (3a)$$

Contingency Curve 2

$$W_1 \doteq \frac{\ln F_2 - \ln k_2 x_2}{\alpha_{21} \ln (1 - q_{21})} - \frac{\alpha_{22} \ln (1 - q_{22})}{\alpha_{21} \ln (1 - q_{21})} W_2. \quad (3b)$$

Equations (3a) and (3b), already presented in abbreviated form as equations (1a) and (1b), provide the postulated linear relationships between W_1 and W_2 required to keep error in contingencies 1 and 2 down to a tolerable level. Equation (3a) gives the relationship for contingency 1, and (3b) for contingency 2.

These equations are based on one set of simple, explicit conditions. The object in deriving them, however, is not to make a guess about the precise relationships but, rather, to illustrate the general form they are expected to take. The only crucial result for the deductions to be made in Figures 2-7 is that the relationships can be put in a linear form. Equations (3a) and (3b) are of course in linear form, but they were derived from a particular hypothesis. It is easy, on the other hand, to show that the conditions can be greatly relaxed, or the graphical coordinates transformed, to provide a linear graphical representation of the kind to be used in Figures 2-7. For instance, suppose the number of contacts per caste per contingency were not linearly related to the weight W_i of the caste, that is, the number could not be expressed as $\alpha_{1i}W_i$, but was related in some other way, for example, as some logarithmic function of W_i . As long as the function is the same for the two castes, the contingency curves would still be linear. Next, even if the contingency curves are not linear algebraically, they can in a great many cases be made linear by transformations of the W_1 and W_2 axes. Finally, if the curves still cannot be made linear by any transformation, it should still be possible to conduct analyses on segments of the curves that are approximately linear.

In conclusion, we do not yet know the shape of real contingency curves, and to attempt a guess at their precise form would be inappropriate, except for illustrative purposes as undertaken here. On the other hand, it is a much more reasonable proposition that contingency curves can be presented as straight lines in a generalized graphical form, with or without transformation of the axes. When this is done, new insight can be gained into the possibilities of social organization in insects. But before the next step is taken, a brief discussion of certain special biological qualities of insect societies is needed.

Special Qualities of Insect Societies Put into the Model

The procedure of making the behavioral responses probabilistic may seem strange at first, but it has a sound biological rationale. To make this point clear, we might ask why the model was not constructed in a more straightforward manner by having members of different castes laboring at their assigned tasks through the day and night, producing to the utmost of their hexapodan capacities. Then the more conventional procedures of linear programming would have been easy to apply. But social insects simply do not behave that way. Contrary to folklore, most of the members of an insect colony are idle at any given moment, and the greater part of the life of each individual is spent in relative quietude. The members of colonies respond to contingencies, which can be identified as discrete, albeit very numerous, events, much as visualized in this model. Abundant documentation for the point is provided by studies cited in the recent reviews of Lindauer (1961) and Wilson (1966).

A second special feature that needs comment is the way cost is assessed.

In the model the colony is given a certain period of time to accomplish the task presented by the contingency; if it fails, it takes the penalty in reduced queen production. This would be the case for such contingencies as intrusion by a predator, which could result in the loss of one or more colony members, or self-fouling by a larva, which could result in the death of the larva. It is also easy to accommodate more complex, and perhaps more general, cost functions without seriously affecting the qualitative conclusions about to be made. For example, suppose the task remains undone until a member of the correct caste comes upon the contingency, that is, a contingency of type 1 requires an encounter by a member of caste 1. Then on the average the $[(\alpha_{11}W_1 + \alpha_{12}W_2)/\alpha_{11}W_1]$ th worker encountering the contingency belongs to the correct caste (caste 1); and, where t is the average interval between encounters by workers of all castes, the mean time elapsing before the task is done is $t[(\alpha_{11}W_1 + \alpha_{12}W_2)/\alpha_{11}W_1]$. The cost would then be some function of this mean elapsed time. Actually, a reasonable estimate of cost as a function of caste ratios can only be accomplished empirically. It will be a necessary prelude to making this or any other programming model predictive for specific cases.

RESULTS

The optimal mix of castes is the one which gives the minimum summed *weights* of the different castes while keeping the combined cost of the contingencies at the maximum tolerable level. The manner in which the optimal mix is approached in evolution is envisaged as follows. Any new genotype that produces a mix falling closer to the optimum is also one that can increase its average net output of queens and males. In terms of energetics, the average number of queens and males produced per unit of energy expended by the colony is increased. Even though colonies bearing the new genotype will contain about the same adult biomass as other colonies, their average net output will be greater. Consequently, the new genotype will be favored in colony-level selection, and the species as a whole will evolve closer to the optimal mix.

The general form of the solution of the optimal mix problem for the case of two contingencies and two castes is given in Figure 2. It has been postulated that behavior can be classified into sets of responses in a one-to-one correspondence to a set of kinds of contingencies. Even if this conception only roughly fits the truth, it can be used to develop a theory of ergonomics. Not all kinds of contingencies occur frequently enough, or are important enough when they occur, to evoke the evolution of a distinct response. Those that do, I have suggested here, are handled by the colony in such a way that in the end they decrease fitness only by a certain threshold amount, with the same amount being permitted to each kind of contingency separately. From suitable modifications of the graphical model of Figure 2, a series of theorems can be drawn:

1. By inspection of Figures 3 and 4, it can be seen that, as long as the

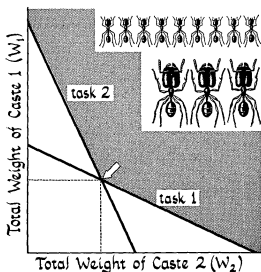


FIG. 2.—The case of two contingencies dealt with by two castes. The optimal mix for the colony, measured in terms of the respective total weights of all the individuals in each caste, is given by the intersection of the two curves (from equations 3a and 3b). Contingency curve 1, labeled "task 1," gives the combination of weights (W_1 and W_2) of the two castes required to hold losses in queen production to the threshold level due to contingencies of type 1; and contingency curve 2, labeled "task 2," gives the combination with reference to contingencies of type 2. The intersection of the two contingency curves determines the minimum value of $W_1 + W_2$ that can hold the losses due to both kinds of contingencies to the threshold level.

contingencies occur with relatively constant frequencies, it is of advantage for the species to evolve so that in each mature colony there is one caste specialized to respond to each kind of contingency. In other words, one caste should come into being which perfects the appropriate response, even at the expense of losing proficiency in its response to other kinds of contingencies.

2. Figure 5 demonstrates that if one caste increases in efficiency in the course of evolution, and the others do not, the proportionate total weight of the improving caste will decrease. In other words, the expected result of group selection is precisely the opposite of that of individual selection, which would be an increase in the more efficient form. The decrease in weight is proportional to the increase in specialization and (inversely) to the slope of the opposite contingency curve. More precisely, as seen in Figure 5, the increase in specialization of caste 1 with reference to task 1 is measured by the ratio of intercepts a/a' , while the decrease in weight is measured by b/b' . Then, by similar triangles, $a/\omega = b(\omega - \beta)$ and $a'/\omega = b'(\omega - b')$, and from these relations

$$\frac{a}{a'} = \frac{(\omega - \beta')}{(\omega - \beta)} \frac{b}{b'}$$

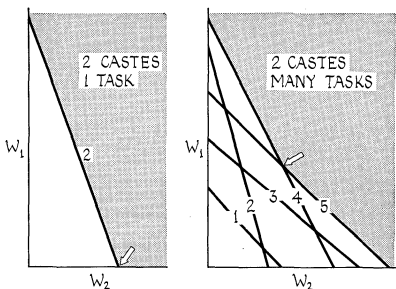


FIG. 3.—*Left*: When there are more castes than tasks, the number of castes will be reduced in evolution to equal the number of tasks. The surplus castes removed will be the least efficient ones (in this case, caste 1). *Right*: If there are more tasks than castes, the optimal mix of castes will be determined entirely by those tasks, equal or less in number to the number of castes, which deal with the contingencies of greatest importance to the colony in terms of average productivity of virgin queens and males (in this case, tasks 4 and 5).

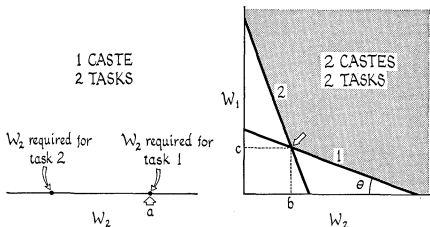


FIG. 4.—It is always to the advantage of the species to evolve new castes until there are as many castes as contingencies and each caste is specialized uniquely on a single contingency. This theorem can be substantiated readily from a comparison of the two graphs in this figure. With the addition of caste 1, the total weight of workers is changed from a to $b + c$. Since caste 1 specializes on task 1, θ is acute, therefore $a - b > c$ and $a > b + c$ for all a , b , and c .

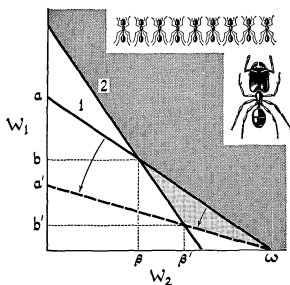


FIG. 5.—If one caste increases in efficiency, and the others do not, the proportionate total weight of the improving caste will decrease. Compare with Fig. 2.

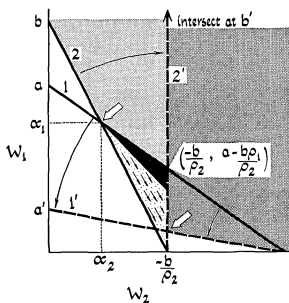


FIG. 6.—An increase in specialization of a given caste will result, under most conceivable circumstances, in increased efficiency and colony fitness. As specialization occurs through evolution, in this imaginary example in caste 1, the slope of the contingency 1 curve decreases, while the slope of the contingency 2 curve may or may not increase (but it does not decrease). (Further explanation in the text.)

The graphical presentation of Figure 6 demonstrates that there are conditions under which any increase in specialization, involving even a total loss of capacity in every other contingency, will increase colony fitness. Under certain other conditions, on the other hand, an increase in specialization at the favored task will, if accompanied by loss of capacity in other tasks beyond a certain degree, result in loss in colony fitness. But any increase in specialization not accompanied by a loss of capacity in other tasks will result in increased colony fitness. To be more specific, a change in specialization of a caste involves a shift in one or (more likely) both contingency curves. As shown in Figure 6, the intersection of the curves move to some point in the "sweep-out" triangle. A move into the stippled part of the triangle results in less total weight for both castes combined and hence greater ergonomic efficiency. A move into the blackened part of the triangle results in equal or greater total weight for both castes combined and equal or less ergonomic efficiency. Under certain conditions, explained in Appendix I, the evolving species loses colony efficiency if, while improving a caste at one task, it permits the caste to reduce ability at performing other tasks. But interestingly there are other conditions under which any specialization increases efficiency; that is, the black triangle does not exist.

The inferences from the models of Figures 5 and 6 can be summarized in the following simplified way: In a constant environment, caste determination should evolve so that each caste becomes increasingly specialized to its single assigned task.

3. If proliferation and divergence of castes are the expected consequences of selection at the colony level, why have they not reached greater heights throughout the social insects? In fact, these qualities vary greatly from group to group and even from species to species within the same taxonomic group. The only answer consistent with the theory is that, as in most evolving systems, the various levels reached by individual species are compromises between opposing selection pressures. The obvious pressure that must oppose proliferation and divergence is fluctuation of the environment. From Figure 7 we can see that a long-term change can eliminate a caste if the caste that supersedes it (by taking over its task through superior numbers) is not very specialized. In this example, contingency 2 has been increased in frequency (or importance), shifting the contingency curve to the right of the contingency 1 curve intercept of the W_2 axis. Consequently, the number of caste 2 workers required to take care of contingency 2 is also more than enough to take care of contingency 1. The presence of caste 1 now reduces colony fitness, and if the environmental change is of long duration, caste 1 will tend to be eliminated by colony-level selection. In this case the species tracks the environment to acquire a new optimal mix that just happens to eliminate the superseded caste. Thus if the critical features of the environment are changing at a rate slow enough to be tracked by the species but too fast to permit much

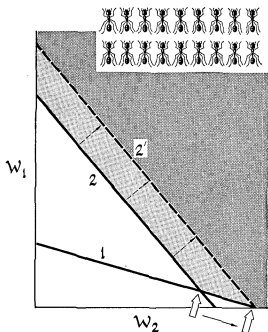


FIG. 7.—A long-term change in the environment can cause the evolutionary loss of a caste, even when the task to which the caste is specialized remains as common and important as ever.

specialization of individual castes, both the number and the degree of specialization of castes will be kept low.

At another level, the critical features of the environment may be changing too fast to be tracked genetically, yet too slow to provide each colony with a consistent average for the duration of its maturity. In this case, a mix of specialized castes would be inferior to a few generalized forms able to adapt to new circumstances.

In Figures 8 and 9 a relation is shown to exist between the degree of caste specialization and the magnitude of change in the optimal mix which is invoked by a given change in the environment. The castes represented in Figure 8 are relatively unspecialized. Task 2 is shown to become somewhat less common (or less important), resulting in a shift of the contingency curve toward the origin without a change in slope. As a consequence, the optimal mix changes from one comprised predominantly of caste 2 to one comprised predominantly of caste 1. In contrast, the castes represented in Figure 9 are highly specialized; and a shift in the contingency curve results in little change in caste ratios.

From the models presented in Figures 7-9, we can draw the conclusion that species with unspecialized castes will have on the average fewer castes and more variable caste ratios, and this effect will be enhanced in fluctuating environments. The more specialized the castes become, the more entrenched

they become, in the sense that they are more likely to be represented in the optimal mix regardless of long-term fluctuations in the environment. Here we have another, peculiar theoretical result of group selection; for, in

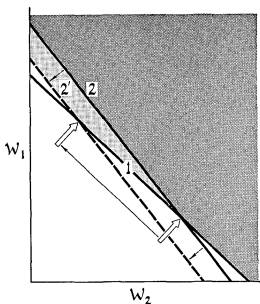


FIG. 8.—If the castes are relatively unspecialized, small changes in the environment will result in large changes in the optimal caste ratios.

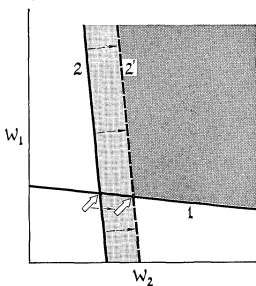


FIG. 9.—The more specialized the castes are in aggregate, the less change there is in the optimal mix.

classical population genetic theory, which entails individual selection, it is the generalized genotypes and species and not the specialized ones that are the more likely to survive in the face of long-term fluctuation in the environment.

EMPIRICAL EVIDENCE

No contingency curves of actual species have yet been drawn. At the moment, the required steps of defining contingencies and measuring their effects in natural populations seem technically formidable. Yet I can see no way of probing very deeply into the evolution of castes except by this means, or at least by comparable studies guided by an ergonomic theory equivalent to the one offered here.

Turning to empirical information already available, we find that temporal division of labor in insect societies has not been studied enough to permit a comparison of "castes," as broadly defined, among species and thus to identify evolutionary trends of relevance to the theory. In order to test the predictions of the ergonomic models in any manner, it is necessary for the moment to fall back on available data concerning the purely physical castes. Even this kind of evidence has an important limitation. Worker subcastes are known only from ants and termites. They are usually, although not always, produced by a partition of the workers into a soldier subcaste concerned primarily with defense and a minor worker (or pseudergate, etc.) subcaste devoted to the remaining functions. These special conditions make generalizations from physical castes to temporal castes an uncertain step.

Nevertheless, the evidence from the physical castes does seem compatible with the theory. We can recognize at least four phenomena that are better explained by the present formulation than by any other, earlier explanations.

First, it turns out that the soldier caste has been lost secondarily in some polymorphic ant lines, even where the defensive function surely still exists (see Wilson, 1953). The possibility of just such an occasional paradoxical development is predicted in Figure 7.

Second, physical castes are more frequent in tropical ant faunas than in temperate ant faunas. This correlation, which I do not believe has been investigated by previous authors, is documented in Appendix II. It is consistent with the notion that castes always tend to proliferate in evolution but are simultaneously being reduced in response to fluctuations in the environment, the degree of response being proportionate to the degree of fluctuation.

Third, the most specialized castes are found primarily in tropical genera and species. The bizarre soldiers of ant genera such as *Paracryptocerus*, *Pheidole* (*Elasmopheidole*), *Acanthomyrmex*, *Zatapinoma*, *Camponotus* (*Colobopsis*), and of termite genera such as *Nasutitermes*, *Mirotermes*, and *Capritermes* are all but limited to the tropics and subtropics. Polymorphism in temperate ant species, representing the less extreme members

of *Pheidole*, *Solenopsis*, *Monomorium*, *Myrmecocystus*, and *Camponotus*, is predominantly of the simpler form produced by elementary allometry. This climatic correlation is consistent with the prediction from ergonomic theory that specialization in castes already in existence should increase indefinitely until countered by opposite selection pressures imposed by fluctuations in the environment.

Finally, it is my subjective impression—but principally from field observations and so far unsupported by quantitative data—that, among ant species, the more anatomically specialized the caste, the scarcer it is. If proven true, this relation would be consistent with the result given in Figure 5 and in fact would be difficult to explain by any other hypothesis.

SUMMARY

The analysis of caste ratios and their effect on colony efficiency can be approached by linear programming models. In the formulation offered here, account has been taken of certain general features of organization and behavior peculiar to insect societies; selection was assumed to be at the colony level; and the optimization goal was given as the maximum production of new queens and males by a mature colony whose size has an upper limit characteristic of the species. Even in their elementary form, the linear models here produced some interesting new conclusions, among which are the following:

1. Different kinds of contingencies, for which distinct behavioral responses are evolved (e.g., invasion by enemies, larval hunger, nest fouling), will be met by the colony as a whole in such a way that each kind of contingency causes about the same amount of reduction in average queen production.

2. Castes, including both physical variants and temporal behavioral stages, will tend to be proliferated in evolution until there is one and only one distinct caste specialized to meet each contingency.

3. The weight of workers belonging to a given caste at a given moment will increase in evolution according to the frequency and importance of the contingency to which it is specialized.

4. Under most, but not all, circumstances, it is of advantage to the colony progressively to increase the degree of specialization of each caste.

5. The more specialized the caste becomes, and in general the more efficient it becomes, the less will be its representation in the colony. This inverse relation between ability and numbers, which is a consequence of selection at the colony level, is the direct opposite of what would be predicted from selection at the level of the individual organism.

6. Proliferation of castes should be countered by those contingencies whose changes in frequency through time are poorly autocorrelated and paced so as to be difficult to track genetically. Certain changes in the environment can result in a caste being dropped, a result that at first seems paradoxical. This is due to the fact that, even though the caste is still the

best one to handle a contingency that continues to be important, its presence nonetheless results in lowered efficiency of the colony as a whole.

7. The more specialized a caste has become, the less likely it is to be dropped from the optimal mix due to fluctuation in the environment. This, too, is the opposite of what would be expected if selection were operating at the level of the organism rather than at the colony level.

8. Certain empirically determined qualities of physical castes in ants and termites are consistent with the result of this ergonomic theory and, for the moment at least, seem best explained by it.

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APPENDIX I

A FULLER ACCOUNT OF THE CONSEQUENCES OF CASTE SPECIALIZATION

Following is a fuller explanation of the principles expressed under Figure 6.

Let ρ_1 be the slope of the contingency 1 curve before evolution and ρ_1' the slope afterward; and ρ_2 the slope of the contingency curve 2 before evolution and ρ_2' afterward. Specialization on the part of caste 1 means that it becomes more efficient at task 1, so that $\rho_1 \rightarrow \rho_1'$ must involve a decrease. On the other hand, the specialization to task 1 may or may not result in caste 1 becoming less efficient at task 2; if there is any change at all, $\rho_2 \rightarrow \rho_2'$ therefore involves an increase.

A mandatory decrease in ρ_1 and an optional increase in ρ_2 results in the intersection of contingency curves 1 and 2 moving down and to the right. A new value is reached which is one of a large convex set of values bounded by the triangle whose coordinates are (α_1, α_2) , $[-b/\rho_2, a - (b\rho_1/\rho_2)]$, and some values near but not equal to $[-(b/\rho_2'), 0]$. The second and third apexes are set by the 2' curve being rotated until it becomes parallel with the W_1 axis. This is what would happen in the extreme case of caste 1 losing all ability to perform function 2.

Now let us define the stippled part of the sweep-out triangle. Before evolution, the combined weight of the castes is $\alpha_1 + \alpha_2$, the sum of the coordinates of the upper left apex of the triangle. This apex is simply the intersection of the original contingency curves, so that α_1 and α_2 are related as follows:

$$\alpha_1 = a + \rho_1 \alpha_2,$$

$$\alpha_1 = b + \rho_2 \alpha_2.$$

Solving for α_1 and α_2 and then adding them,

$$\alpha_1 = \frac{\rho_2 a - \rho_1 b}{\rho_2 - \rho_1},$$

$$\alpha_2 = \frac{a - b}{\rho_2 - \rho_1},$$

$$\alpha_1 + \alpha_2 = \frac{a - b + \rho_2 a - \rho_1 b}{\rho_2 - \rho_1}.$$

If $\alpha_1 + \alpha_2$ is greater than the sum of the coordinates of the point within the sweep-out triangle reached by increased specialization, the colony has reduced the combined weight of caste 1 and 2 and thus increased efficiency. The coordinates and sum of coordinates in the triangle are given by

$$W_1 = a' + \rho'_1 W_2,$$

$$W_1 = b' + \rho'_2 W_2,$$

$$W_1 + W_2 = \frac{a' - b' + \rho'_1 a' - \rho'_2 b'}{\rho'_2 - \rho'_1}.$$

And it follows that, when

$$\frac{a - b + \rho_2 a - \rho_1 b}{\rho_2 - \rho_1} > \frac{a' - b' + \rho'_2 a' - \rho'_1 b'}{\rho'_2 - \rho'_1},$$

the increase in specialization results in increased ergonomic efficiency, while the reverse relation results in decreased efficiency. If a caste increases its capacity to perform one task without losing ability to perform the other task, there will always be an increase in ergonomic efficiency. This is intuitively apparent, and it can be confirmed by noting that under the given condition $b = b'$ and $\rho_2 = \rho'_2$; and since by definition $a > a'$ and

$$\rho_1 > \rho'_1, \quad \frac{a - b + \rho_2 a - \rho_1 b}{\rho_2 - \rho_1} > \frac{a' - b' + \rho'_2 a' - \rho'_1 b'}{\rho'_2 - \rho'_1}$$

always.

Finally, when

$$\frac{a - b + \rho_1 b - \rho_2 a}{\rho_1 - \rho_2} > \frac{a - b\rho_1 + b}{\rho_2},$$

any increase in ability at task 1 increases ergonomic efficiency regardless of the loss of ability at task 2. This result is obtained as follows. The maximum sum of coordinates that can be obtained in any sweep-out triangle is at the outer apex of that particular triangle formed when the evolving caste loses all ability to perform the function to which it is not specialized. This extreme situation is illustrated in Figure 6. The value b' , defined as the weight of caste 1 required to perform task 2 if left by itself, approaches infinity. The coordinates of the outer apex of the sweep-out triangle become

$$\left(-b/\rho_2, a - \frac{b\rho_1}{\rho_2}\right)$$

and their sum is

$$\frac{a - b\rho_1 + b}{\rho_2}.$$

If the sum of the coordinates of the original intersection of contingency curves is greater than this sum, then it is greater than the sum of coordinates of any other point in the triangle.

To summarize the conclusions of this argument, we can define widely ranging conditions under which an increase in caste specialization in an unchanging environment results in greater ergonomic efficiency, and much more limited conditions under which it does not. If we could measure the contingency curves in experiments, and they should prove linear, we could then predict the permissible evolutionary pathways in caste evolution.

APPENDIX II

VARIATION IN FREQUENCY OF SPECIES WITH PHYSICAL WORKER SUBCASTES
("POLYMORPHIC SPECIES") IN DIFFERENT ANT FAUNAS AROUND THE WORLD

The data in Table 1 were compiled from taxonomic studies published by various authors in the past 60 years. While the completeness of the collections on which the studies were based varied greatly, there is no reason to doubt that each represents a random sample of species as far as polymorphism is concerned.

An examination of these data reveals several trends, and lack of trends, of interest. In the New World, the frequency of polymorphic species drops off in both the north and south temperate zones. This is noteworthy because the genera and species are mostly different at the two ends. There is a sharp decline also in going from North Africa to the limits of the ant fauna in northern Europe. A slight decline is apparent in temperate South Africa. Also, a slight decline is seen from the southern to the northern Palaearctic region and from Australia to New Zealand. However, the remainder of the Indo-Australian area does not display the same climatic trend. Tropical Asia and Melanesia have a relatively low frequency of polymorphic species, although not so low as most of the marginal cold temperate regions around the world. There is a local *increase* going north into the Himalayas. There is no apparent trend either way across Australia.

In general, then, there is a decline in polymorphism with increasing coldness of climate everywhere in the world except in the Indo-Australian region. In the Himalayan region the reverse effect is seen.

Perhaps we should expect environments to be more fluctuating on islands and in deserts, and polymorphism to decline accordingly. However, the data show this not to be the case. The frequency of polymorphism on islands is consistent with that on the nearest continent at the same latitude. The faunas of deserts may even increase in polymorphism somewhat. But it appears that the overriding determinant on a global scale is latitude.

In conclusion, the latitude effect is probably clear enough to be regarded as consistent with the prediction from ergonomic theory. On the other hand, the lack of an island or desert effect is not consistent with it—yet does not oppose it.

TABLE 1

Locality	Climate	Total Number of Species	Number of Polymorphic Species	Percentage of Polymorphic Species	Authority
Neotropical:					
Amazonas (state), Brazil.....	Tropical	71	27	38.0	Wheeler (1923)
Galapagos.....	Tropical	19	6	31.6	Wheeler (1924b)
Honduras and Guatemala.....	Tropical	86	32	37.2	Mann (1922)
Haiti.....	Tropical	67	16	23.9	Wheeler and Mann (1914)
Puerto Rico.....	Tropical	60	10	16.7	Smith (1936)
Jamaica.....	Tropical	34	14	41.2	Wheeler (1917b)
Cuba.....	Tropical	74	17	23.0	Wheeler (1913)
Tucuman Prov., Argentina.....	Subtropical	130	45	34.6	Kusnezov (1953)
Hidalgo State, Mexico.....	Warm temperate	37	11	29.7	Wheeler (1914a)
East Patagonia and Tierra del Fuego...	Cold temperate	19	2	10.5	Kusnezov (1959)
Neartic:					
Florida Keys.....	Subtropical	41	12	29.3	Wilson (unpublished)
Welaka Reserve, central Florida.....	Warm temperate	76	13	17.1	Van Pelt (1956)
California.....	Subtropical to warm temperate	94	20	21.3	Mallis (1941)
North Carolina: coastal plain.....	Warm temperate	115	17	14.8	Carter (1962)
North Carolina: mountains.....	Warm to cold temperate	83	12	14.5	Carter (1962)
George Reserve, Michigan.....	Cold temperate	67	5	7.5	Talbot (in Wilson, 1959)
North Dakota.....	Cold temperate	83	8	9.6	G. C. Wheeler and J. Wheeler (1963)
Alaska.....	Cold temperate	12	1	8.3	Wheeler (1917a)
Western Palearctic:					
Tassili des Ajjer, central Sahara.....	Tropical (desert)	45	13	29.0	Bernard (1953)
Canary Islands.....	Subtropical	55	11	20.0	Wheeler (1927c)
Madeira.....	Subtropical	15	2	13.3	Wheeler (1927c)
Manora Forest, Morocco.....	Subtropical	41	12	29.3	Bernard (1953)
Balearics.....	Subtropical to warm temperate	26	7	26.9	Wheeler (1926)

TABLE 1.—Continued

Locality	Climate	Total Number of Species	Number of Polymorphic Species	Percentage of Polymorphic Species	Authority
France: Tourrettes-sur-Loup, south coast	Warm temperate	37	8	21.6	Collingwood (1956)
France: Fontainebleau	Warm to cold temperate	30	1	3.3	Collingwood (1956)
South Lake Dist., England	Cold temperate	17	0	0	Collingwood and Satchell (1956)
Ireland	Cold temperate	16	0	0	Collingwood (1958)
Scottish Highlands	Cold temperate	18	0	0	Collingwood (1961a)
Sweden	Cold temperate	60	4	6.7	Forslund (1957)
Baltic Amber (Eocene)	Tropical to temperate?	92	10	10.9	Wheeler (1914b)
Ethiopian:					
Congo	Tropical	318	91	28.6	Wheeler (1922)
Malagasy	Tropical	237	69	29.1	Wheeler (1922)
Inatong Mts., Sudan: lower slopes	Tropical	99	23	23.2	Weber (1943)
Inatong Mts., Sudan: 5,600 ft and higher	Warm to cold temperate	34	8	23.5	Weber (1943)
Rhodesia	Subtropical	33	5	15.2	Forel (1913a)
Natal, S. Africa	Warm temperate	72	15	20.8	Santschi (1914)
Oriental to Eastern Palearctic:					
Borneo	Tropical	243	58	23.9	Wheeler (1919)
Krakatau Islands (1919-21)	Tropical	65	14	21.5	Wheeler (1924a)
Indochina	Tropical	65	14	21.5	Wheeler (1927b)
Formosa	Tropical to subtropical	68	17	25.0	Forel (1913b); Wheeler (1930)
China	Subtropical to cold temperate	191	39	20.4	Wheeler (1931)
Afghanistan	Mountainous, cold temperate	44	14	31.8	Collingwood (1961b)
Nanga Parbat, NW Himalayas	Mountainous, cold temperate	18	6	33.3	Eidmann (1942)
Japan (entire)	Warm to cold temperate	69	12	17.4	Wheeler (1928)

TABLE 1.—Continued

Locality	Climate	Total Number of Species	Number of Polymorphic Species	Percentage of Polymorphic Species	Authority
Japan: Sapporo.....	Cold temperate	28	6	21.4	Hayashida (1960)
Japan: Mt. Atsutanupuri.....	Cold temperate	11	1	9.1	Hayashida (1959)
West China and Tibet.....	Mostly cold temperate	43	4	9.3	Edmann (1941)
Turkistan.....	Cold temperate	39	7	17.9	Kusnezov (1926)
Hsingan Prov., North Manchuria.....	Cold temperate	7	0	0	Yasumatsu (1941)
Oceania and Australia:					
Buru River, New Guinea.....	Tropical	179	39	21.8	Wilson (1959)
Solomons.....	Tropical	123	19	15.4	Mann (1919)
Fiji.....	Tropical	88	25	28.4	Fullaway (1956)
Wallis-Futuna.....	Tropical	36	7	19.4	Wilson and Hunt (1967)
Polynesia.....	Tropical	35	5	14.3	Wilson and Taylor (1967)
New Caledonia.....	Subtropical	67	17	25.4	Emery (1914)
Lord Howe I.....	Subtropical	14	1	7.1	Wheeler (1927a)
Norfolk I.....	Subtropical	12	1	8.3	Wheeler (1927a)
Australia: Queensland.....	Tropical to subtropical	174	29	16.7	Forel (1915)
Australia: Everard and Musgrave Ranges, center of Australia.....	Warm temperate	30	10	33.3	Wheeler (1915)
Australia: Rottnest I.....	Warm temperate	43	7	16.3	Wheeler (1934)
Australia: southwest.....	Warm temperate	72	15	20.8	Forel (1907)
New Zealand.....	Warm to cold temperate	31	4	12.9	Wilson and Taylor (1967)
Tasmania.....	Cold temperate	20	4	20.0	Forel (1913b)

Note.—In each region, localities are listed with the one farthest from the pole first, then proceed poleward, until the last entry in each category is closest to the pole.

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